Response of Common Murres to the *Exxon Valdez* Oil Spill and Long-Term Changes in the Gulf of Alaska Marine Ecosystem

JOHN F. PIATT

National Biological Service, Alaska Science Center, 1011 East Tudor Road,
Anchorage, Alaska 99503, USA

PAUL ANDERSON

National Marine Fisheries Service, Alaska Fisheries Science Center
P.O. Box 1638, Kodiak, Alaska 99615, USA

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Abstract.—Short-term effects of the 1989 TV *Exxon Valdez* oil spill on seabirds were dramatic and well documented. Seabird populations at sea in the spill zone were immediately depressed, and more than 30,000 dead, oiled seabirds were recovered from beaches within months of the spill. It is estimated that 250,000 seabirds were killed by oil, of which 74% were murres *Uria* spp. Based on comparisons of prespill (1970s) and postspill (1989–1994) data, long-term effects on murres attributed to oil pollution included population declines, reduced breeding success, and delayed breeding phenology. Populations remained depressed, but breeding success and phenology gradually returned to normal levels by 1993. An alternative hypothesis to explain these long-term effects is that murres were responding to natural events in their marine environment. Reduced flow of the Alaska Coastal Current (ACC) in 1989 may have reduced and delayed biological productivity in the ACC. On a broader time scale, marked changes in marine fish communities have occurred during the past 20 years. Coincident with cyclical fluctuations in seawater temperatures, the abundance of small forage species (e.g., northern pink shrimp *Pandalus borealis*, capelin *Mallotus villosus*, and Pacific sandfish *Trichodon trichodon*) declined precipitously in the late 1970s while populations of large predatory fish (e.g., walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*, and flatfish) increased dramatically. Correspondingly, seabird diets shifted from mostly capelin in the 1970s to mostly Pacific sand lance *Ammodytes hexapterus* and juvenile pollock in the late 1980s. Furthermore, a variety of seabirds and marine mammals both inside and outside of the oil spill zone exhibited signs of food stress (population declines, reduced productivity, die-offs) throughout the 1980s and early 1990s. We conclude that available data are inadequate to distinguish between long-term effects of the *Exxon Valdez* oil spill on murres and a natural response of murres to long-term changes in their marine environment.

On 24 March 1989, the TV *Exxon Valdez* grounded in Prince William Sound and spilled 43.9 million liters of crude oil into the marine environment. During the weeks that followed, winds and currents pushed oil out of Prince William Sound and into the Gulf of Alaska, where it eventually drifted 750 km to the southwest (Piatt et al. 1990; Galt et al. 1991). Pre- and postspill aerial surveys of Prince William Sound conducted in 1989 revealed that at-sea populations of loons, grebes, cormorants, and sea ducks declined by 44–84% in the immediate aftermath and trajectory of the spill (Piatt et al. 1990). In the gulf, censuses of murre colonies indicated that numbers were substantially lower (30–65%) at several colonies in 1989 than in previous years (Nysewander et al. 1993).

Between March and August, about 30,000 dead, oiled seabirds were retrieved from beaches (Piatt et al. 1990). Carcasses comprised mostly common murres *Uria aalge* (70%), thick-billed murres *U. lomvia* (4%), other alcids (7%), sea ducks (5.3%), and cormorants (3%). Extrapolating from numbers retrieved and the results of drift experiments, it was estimated that hundreds of thousands of seabirds were actually killed by oil (Piatt et al. 1990; ECI 1991; Piatt and Ford 1996, this volume). This was the highest toll of seabirds from a single oil spill ever documented (Piatt and Lensink 1989; Burger and Fry 1993).

Given these massive losses, Piatt et al. (1990) suggested that effects of the spill on murre populations might extend over many subsequent years because of the changes in demography, production, and recruitment that were predicted by population models (e.g., Ford et al. 1982; Samuels and Lanfear 1982). Furthermore, ingestion of oil by murres could have had some long-term effects on their breeding biology (e.g., Fry et al. 1986). Based on experiences elsewhere (e.g., Stowe 1982; Dunnet 1982), however, it seemed likely that population effects would be difficult to detect beyond the first year of impact (Piatt et al. 1990, 1991).

Various studies designed to assess long-term impacts on seabirds were conducted in the years

(1989–1994) after the *Exxon Valdez* oil spill, some under the auspices of the government-appointed *Exxon Valdez* Trustees Council (this volume), some under the auspices of the Exxon Corp. (Wells et al. 1995). Results of some of these studies suggested that the oil spill may have caused significant population declines, reduced breeding success, and delayed breeding phenology of murres in some colonies. In this overview, we consider results of these studies in light of information about the marine environment in the Gulf of Alaska and provide some alternate hypotheses to explain the observed changes in murre population biology.

Effects of the Spill on Murre Populations

Estimating the Size of Murre Populations

Murre census data must be interpreted with caution. We have no measure of the accuracy or precision of most prespill census data because they were usually gathered during one-time visits to colonies, and methods for censusing murres were not standardized. At least five counts per season at a murre colony are required for reliable ($P < 0.05$) detection of annual population changes on the order of ±25% (Wanless et al. 1982; Hatch and Hatch 1989). Large murre colonies are difficult to census completely in any case. At present, the preferred method is to assess population trends from small subsamples of total colony populations (e.g., Wanless et al. 1982; Piatt and McLagan 1987).

Furthermore, colony counts include only birds found at the colony at the time of censusing. In the case of murres, one bird of each breeding pair attends the nest site while the other forages. The population is also comprised of birds that do not attend the colony in any given year—including failed breeders, nonbreeders, and subadults. During the breeding season, about 1.4 times more murres than the number in attendance at colonies may be found at sea (Piatt and Ford 1993).

The choice of which pre- or postspill data to use in estimating murre population changes can be subjective. Widely varying annual population estimates may reflect real changes in murre populations over time, but they may also result from varying survey methods or conditions at the time of censusing. In the following analyses, we have selected the best census data available to assess population changes that occurred at major murre colonies (Figure 1) both before and after the oil spill (Table 1).

Determining which Colonies were "Affected"

There are no murre colonies within Prince William Sound (Figure 1). Porpoise Rocks and Middleton Island are located to the east and outside the path of the spill (see Piatt et al. 1990 and Galt et al. 1991 for discussion of the spill trajectory). About 25% of the oil escaped Prince William Sound (D. A. Wolfe and coworkers, unpublished data). In early April murres along the Kenai Peninsula (Resurrection Bay, Chiswell Islands) and in lower Cook Inlet (Barren Islands, Gull Island) were exposed to oil while it was still quite fluid, and this is when and where most murres were killed (Piatt et al. 1990). Small amounts of oil drifted south to the eastern side of Kodiak Island, possibly affecting murre colonies there (e.g., Triplet Island).

Effects of oil on murre colonies to the west of Cook Inlet (e.g., Puale Bay, Ugaiushak Island) were probably minimal. In mid- to late-April a series of storms emulsified the oil into "mousse." Between 29 April and 2 May, this mousse (then only 2% of the oil spilled) was swept up onto beaches of the Alaska Peninsula from Cape Douglas to Wide Bay (Piatt et al. 1990; Galt et al. 1991). Evidence suggests that both mousse and carcasses were carried over time by prevailing currents to Puale Bay from a point of origin in lower Cook Inlet (Piatt et al. 1990; Piatt and Ford 1996). Only small traces of oil reached the vicinity of Ugaiushak Island. Oil did not reach the Semidi Islands or coastal colonies farther west.

Murre Population Trends

Murres were the species most affected by the spill. If the total bird toll was 250,000 (Piatt and Ford 1996), then about 185,000 murres were killed. What would be the impact of such a kill on murre populations in the northern Gulf of Alaska? In a preliminary estimate, Piatt et al. (1990) suggested that the gulf murre population was reduced by about 10%. This estimate did not account for the at-sea component of populations associated with colonies (Table 2) and it used a few erroneous colony population estimates reported in Sowls et al. (1978). Including the at-sea component, and using revised historical colony estimates (Table 2), estimated losses (185,000 murres) comprised 7.0% of total prespill gulf populations (2,654,640 murres) and 41% of prespill populations in the oiled zone (446,200 murres). Actual censuses conducted after the spill suggest that murre populations in oiled areas declined by 40% and total gulf populations declined by 27% (Table 2).
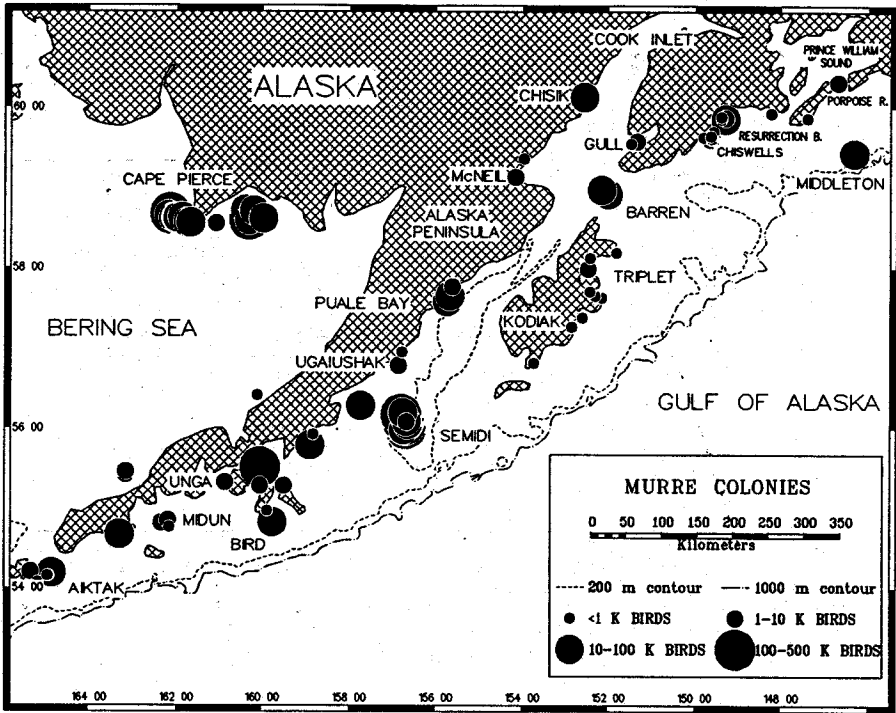
FIGURE 1.—Locations of common murre colonies in the Gulf of Alaska. The indicated colony sizes (K = 1,000) are based on census data obtained before the *Exxon Valdez* oil spill.

Nysewander et al. (1993) suggested that "since populations of murres at colonies [Middleton and Semidis] just outside the trajectory of the oil did not decline following the spill . . . it seems likely that oil mortality caused the population declines at affected colonies." It is tempting to conclude that the loss (−41%) estimated from recoveries of dead murres accounts fully for the observed decline (−40%) at "affected" colonies. However, this is probably coincidental because lower Cook Inlet is a regional "hotspot" that attracts large numbers of seabirds year-round (Gould et al. 1982; Piatt 1994), and it is likely that murres (particularly nonbreeders and subadults) from "unaffected" colonies outside the spill zone were among those killed. Furthermore, population declines occurred at "affected" colonies before the spill and at "unaffected" colonies well outside the range of the spill (Table 1).

More specifically, for colonies located within the path of the spill, major declines occurred (Figure 2) at Resurrection Bay, the Chiswell, Barren, and Triplet islands, and Puale Bay, but not at Gull Island. The average (unweighted by colony size)

decline at these oiled colonies was −30%. However, at 10 colonies outside the spill path (Table 1; Figure 2), the average decline was even greater (−49%). The decline at Middleton Island represents only the most recent situation, because populations increased by about 14% between 1978 and 1988 (Hatch and Piatt 1995). Overall, however, the population decreased by 20% between 1978 and 1991.

Murre populations at the Semidi Islands appeared to be relatively stable over the time period (1975–1991) for which data are available. The Semidis may not be typical of other gulf colonies for several reasons. They are situated along the deep Shelikof trench (Figure 1), and wide-ranging murres forage over a large expanse of shelf and oceanic habitats (Gould et al. 1982; J. Piatt, unpublished data). The high diversity and abundance of breeding bird populations (Hatch and Hatch 1983, 1990a) and diversity of foraging habitats and prey types (Hatch and Hatch 1990b; Hatch and Sanger 1992; Piatt, unpublished data) all indicate that the Semidis are exceptional and stand in contrast to most coastal colonies that are relatively depauper-

TABLE 1.—Population size (individuals in attendance) of large (thousands) murre colonies in the northern Gulf of Alaska before and after the *Exxon Valdez* oil spill in 1989. Prespill changes were calculated from at least two census counts up to and including 1988. Postspill changes were calculated from the most recent census counts conducted before 1989 and counts conducted in 1989–1994. Values in parentheses are means of data from two or more consecutive years. "Years" indicate earliest and latest years of census data used in this analysis.[a]

Area	Years	Prespill change[b]		Postspill change	
		Number of birds	Percent	Number of birds	Percent
Middleton Island	1975–1991	(5,793) to (6,578)	+12%	(7,736) to (5,226)	−32%
Porpoise Rocks	1976–1991			(1,275) to 1,241	−3%
Resurrection Bay[c]	1976–1991			11,170 to 8,384	−25%
Chiswell Islands[c]	1976–1991			3,756 to (2,516)	−33%
Gull Island[c]	1984–1990	(2,323) to 5,500	+136%	5,500 to (5,125)	−7%
Chisik and Duck Islands	1978–1994	10,000 to 4,101	−59%	4,101 to (2,968)	−28%
McNeil Island	1976–1991	2,500 to 2,000	−20%	2,000 to 200	−90%
Barren Islands[c]	1975–1993			70,000 to (46,143)	−34%
Triplet Island[c]	1975–1989	(1,248) to 1,300	+4%	1,300 to 843	−35%
Puale Bay[c]	1976–1991	100,500 to 74,500	−26%	74,500 to (38,784)	−48%
Ugaiushak Island	1976–1991			8,340 to (5,073)	−39%
Semidi Islands	1977–1991	2,816 to 2,856	+1%	(2,613) to (2,973)	+12%
Bird Island	1973–1993			24,000 to 3,620	−85%
Unga Island	1973–1994			6,000 to 232	−96%
Midun Island	1978–1994			3,800 to 1,277	−57%
Aiktak Island	1981–1990			15,000 to 4,000	−73%

[a] All counts are whole-island censuses except for the Semidi Islands, which are counts of murres on plots. Census data are from the following sources and references therein: Sowls et al. (1978); Nysewander et al. (1993); Erickson (1995); Roseneau et al. (1994); USFWS, unpublished data files; S. A. Hatch, unpublished data (Middleton and Semidi Islands); J. Piatt, unpublished data (Bird, Unga, and Midun Islands), L. Slater, USFWS, unpublished data (Chisik and Gull Islands); and G. V. Byrd, USFWS, unpublished data (Aiktak Island).
[b] Absence of data in this column means data not available or not adequate for estimating prespill changes in population size.
[c] Colonies within the path of the spill (Piatt et al. 1990; Nysewander et al. 1993).

ate in seabird and prey species and are influenced primarily by a single water mass, namely, the Alaska Coastal Current (ACC) (Reed and Schumacher 1986). On the other hand, the breeding success of kittiwakes on the Semidis is often concordant with kittiwakes at coastal colonies (Hatch et al. 1993).

Owing to an influx of oceanic water from deep waters to the east, and tidal mixing at the mouth of Cook Inlet, the Barren Islands also support a diverse and abundant mix of seabird species (Piatt 1994). Similarly, Middleton Island provides access to productive shelf–edge habitat and oceanic prey (Hatch 1984; S. Hatch, National Biological Service, unpublished data). Like the Semidis, these colonies may not always reflect processes occurring in the ACC, but are often concordant with other gulf colonies with respect to kittiwake population biology (Hatch et al. 1993).

There is indirect evidence for oil spill effects on populations at some colonies. Boersma et al. (1995) noted a 21% increase in murre numbers on attendance plots at the Barren Islands (East Amatuli) between 1990 and 1991. Such a large "recovery" would be expected if postspill attendance on newly vacant ledges was supplemented by immigration from outside populations or higher recruitment of first-time breeders (Stowe 1982; Boersma et al.

TABLE 2.—Estimates of total murre populations in the northern Gulf of Alaska before (1975–1988) and after (1989–1994) the *Exxon Valdez* oil spill. Percentage changes in populations were calculated from the weighted (by colony size) average changes observed at individual colonies within each area (see Table 1).

Area	Prespill murre population	Change (%)	Postspill murre population
Middleton Island	7,740	−32	5,230
Prince William Sound and Kenai Peninsula[a]	16,410	−25	12,310
Cook Inlet[a]	81,600	−33	54,440
Kodiak Island[a]	5,070	−35	1,770
Puale Bay[a]	74,500	−48	38,780
Ugaiushak Island[a]	8,340	−39	5,070
Semidi Islands	567,090	+12	635,140
Alaska Peninsula	328,850	−85	49,330
East Aleutians	16,500	−73	4,460
Colony totals			
Oiled areas[a]	185,920	−40	112,370
Gulf of Alaska	1,106,100	−27	806,520
At-sea totals[b]			
Oiled areas[a]	260,290	−40	156,170
Gulf of Alaska	1,548,540	−27	1,130,430
Combined totals			
Oiled areas[a]	446,210	−40	268,540
Gulf of Alaska	2,654,640	−27	1,936,950

[a] Areas assumed to be affected by oil.
[b] That part of the population (nonattending breeders, failed or nonbreeders, and subadults) found at sea and not counted during colony censuses (see text).
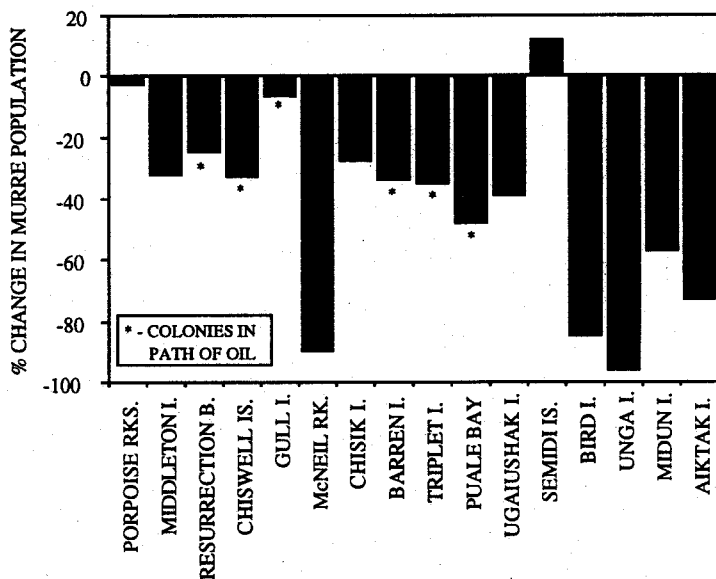
FIGURE 2.—Estimated changes in population size of common murre colonies in the Gulf of Alaska based on post- and prespill comparisons of colony census data (see also Figure 1, Table 1, and text).

1995). Similar postspill "recoveries" were noted at the Chiswell Islands (+28%), Barren Islands (Nord, East Amatuli, and Light Rock plots; +35%), and Puale Bay (+66%) by Nysewander et al. (1993) between 1989 and 1991. Changes of this magnitude (+21 to +66%) are larger than expected from normal annual variation at murre colonies (<15% per annum; Wanless et al. 1982; Harris et al. 1983; Piatt and McLagan 1987; Hatch and Hatch 1989). Postspill increases at the Semidi Islands (+10%, 1989–1991) were within the range of normal variation.

In summary, evidence for effects of the spill on murre populations is not conclusive. The accuracy of most historical census data and estimates of actual mortality from the spill are unknown. We cannot be certain of the degree to which different colonies were "affected" because the quality and toxicity of the oil changed over time, and large numbers of murres from "unaffected" colonies could have been killed while foraging in the spill zone. For this and other reasons, the Semidi and Middleton islands are probably not valid control colonies. Postspill "recoveries" at some affected colonies provide indirect evidence for oil spill effects. Murre populations were declining at some colonies before the spill, and major declines have occurred during the past 20 years at 13 of 16 major

colonies in the northern Gulf of Alaska—8 of which were outside the spill zone, which suggests that other factors have contributed to declines of murre populations in the gulf.

Common Murre Breeding Success and Phenology

Prespill data from the Barren Islands and data collected there in 1989 and 1990 were not adequate to accurately estimate breeding parameters in murres (e.g., see Gaston et al. 1983; Hatch and Hatch 1989), thus, results must be interpreted with caution (Roseneau et al. 1994; Boersma et al. 1995). More extensive studies at the Barrens in 1993–1994 (Roseneau et al. 1994; D. G. Roseneau, U.S. Fish and Wildlife Service, personal communication), Puale Bay in 1989–1992 (J. H. McCarthy and D. A. Dewhurst, U.S. Fish and Wildlife Service, unpublished data), and the Semidi Islands before (Hatch and Hatch 1990a, 1990b) and after (Nysewander et al. 1993) the spill provide an accurate assessment of breeding success and phenology at these colonies.

Breeding success (chicks per site) on the Semidi Islands in both prespill (0.48–0.64) and postspill (0.52–0.60) years was close to average for common murres in Alaska (0.64 ± 0.14 [SD]; Byrd et al. 1993), as was prespill breeding success on the Bar-
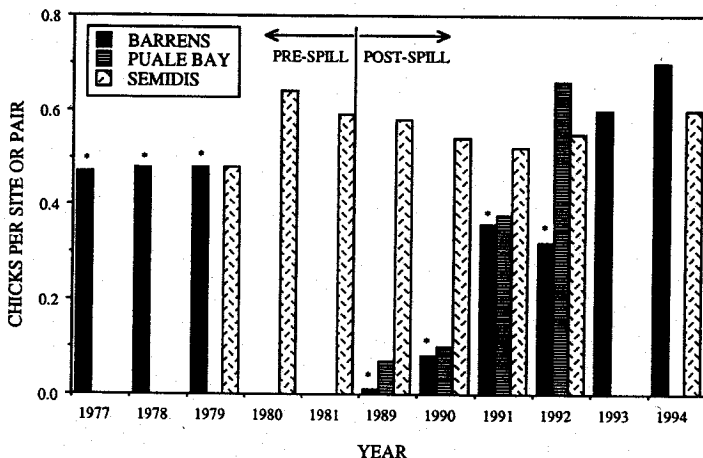
FIGURE 3.—Productivity of common murres at colonies in the Gulf of Alaska, 1977–1994. Barren Islands data in 1977–1980 is from D. A. Manuwal (U.S. Fish and Wildlife Service, unpublished data); in 1989–1992 from Nysewander et al. (1993) and Boersma et al. (1995); and in 1993–1994 from Roseneau et al. (1994). Estimates (Nysewander et al. 1993; Boersma et al. 1995) from Barren Islands in 1990 and 1991 were averaged; in 1992 only Nysewander et al. (1993) data was used. Puale Bay data is from J. H. McCarthy and D. A. Dewhurst (U.S. Fish and Wildlife Service, unpublished data). Semidis data is from Hatch and Hatch (1990b), Nyeswander et al. (1993) and J. Piatt (unpublished data). Asterisks indicate approximate or minimum values because of limited data collection (see text).

ren Islands (approximate minimum estimates; Figure 3). Phenology of first egg-laying on the Semidi and Middleton islands was likewise similar in years before (5–14 June) and after (9–24 June) the spill. First egg-laying at coastal murre colonies (Barren, Chisik, Hinchinbrook, and Ugaiushak islands) in the Gulf of Alaska before (1976–1979) the spill occurred between 17 and 30 June (Nysewander et al. 1993). These data indicate that hatching in prespill years usually occurred in late July through early August (Hatch and Hatch 1990a).

In years immediately after the spill, murres at "affected" colonies exhibited lower breeding success (Figure 3) and later breeding phenology (about 2–4 weeks) than murres in prespill years (Nysewander et al. 1993; Boersma et al. 1995; McCarthy and Dewhurst, unpublished data). Breeding success at sites on the Barren Islands (minimal data; Nysewander et al. 1993) and at Puale Bay was very low in both 1989 (<0.07 chicks/site) and 1990 (<0.10 chicks/site). In 1990, Boersma et al. (1995) also observed low levels of breeding success (about 0.15 chicks/site) on a 5 × 5-m plot at the Barrens. Breeding success recovered markedly in 1991 at the Barrens (0.47–0.72 chicks/site; Boersma et al. 1995) and at Puale Bay (0.48 chicks/site). In 1992, breeding success was higher still at Puale Bay (Figure 3). By 1993 and 1994, breeding success at the Barrens had

returned to normal levels (about 0.6–0.7 chicks/site; Roseneau et al. 1994; Roseneau, personal communication).

After the spill, the onset of egg-laying at the Barren Islands and Puale Bay was later than in prespill years, occurring in early to mid-July (Nysewander et al. 1993; Boersma et al. 1995). In 1989–1991, median hatching dates for common murres were 20–23 d later at Puale Bay (4–13 September; McCarthy and Dewhurst, unpublished data) than at the Semidis (23–26 July) and at least 1 month later than normal for murres in the Gulf of Alaska (above). Median hatching dates at the Barrens were much earlier in 1993 (15–19 August) and 1994 (early to mid-August)—again suggesting a return to normal breeding conditions at the Barrens (Roseneau et al. 1994; Roseneau, personal communication).

Nysewander et al. (1993) advanced two hypotheses to explain the reduction of murre breeding success and delayed phenology at "affected" colonies in 1989–1991. First, the density of murres on breeding ledges may have been reduced drastically by the spill, leading to a reduction in breeding synchrony and success, which are often correlated with density (Birkhead 1977; Harris and Wanless 1988). Second, oil spill losses occurred early in the breeding season and therefore may have affected mostly experi-

enced, adult breeders that return earlier to colonies than subadults (Birkhead 1977; Birkhead and Hudson 1977); this could have led to an increase in the proportion of inexperienced first-time breeders, which typically breed later and have lower breeding success compared to experienced murres (Birkhead and Hudson 1977; Gaston 1991; DeForest 1993). Unfortunately, there is no way to test either of these hypotheses because no data were collected to determine if age-classes were disproportionately affected by oil or whether pre- and postspill densities of murres on ledges were different.

An alternative hypothesis is that oil toxicity might have reduced breeding success in 1989 (Ainley et al. 1981; Trivelpiece et al. 1984) and perhaps the following year (Fry et al. 1986). It seems unlikely that toxic effects would have continued for three to four summers after the spill (Butler et al. 1988).

Another alternative hypothesis is that reduced breeding success and delayed phenology were caused by abnormal environmental conditions at the time of the spill. Breeding parameters at the Semidi Islands after the spill were within the range of prespill values there, but the Semidis may not be typical (see above) of most coastal murre colonies under the influence of the Alaska Coastal Current (ACC). It is more instructive to contrast observations at "affected" colonies with data on murres at Cape Pierce in Bristol Bay (Figure 1) and Bluff in Norton Sound. Although distant from the oil spill zone, these colonies are also bathed by the ACC, which enters the Bering Sea at Unimak Pass and flows north along the coast as far as the Chukchi Sea (Springer et al. 1984). Both colonies have similar seabird and forage fish communities to those found in ACC waters of the Gulf of Alaska (Springer et al. 1984, 1987; Murphy et al. 1986, 1991; L. M. Haggblom, U.S. Fish and Wildlife Service, unpublished data).

Murres at both Cape Pierce and Bluff also exhibited delayed phenology and reduced breeding success in 1989. At Cape Pierce, mean hatching was 27 d later in 1989 than it was in 1993, and, similarly to "affected" gulf colonies, hatching occurred progressively earlier from 1989 to 1993 (Haggblom, unpublished data). In 6 years (1989–1994) of study, breeding success was lowest in 1989 (0.47 chicks/site versus 0.55–0.64 chicks/site). During 5 years (1987–1991) of study at Bluff (Murphy and Schauer 1996), median fledging of murre chicks occurred later in 1989 (28 August) than in any other year (12–17 August), and breeding success was lowest in 1989 (0.51 chicks/site versus 0.66–0.78 chicks/site).

What natural factors might explain these obser-

vations at murre colonies in the ACC? Seawater temperatures in the Gulf of Alaska were not unusually warm or cold in 1989–1991 compared to surrounding years (Figure 4; Royer 1993). Owing to a major reduction of freshwater input in the Gulf of Alaska, however, the estimated transport of the ACC was lower in 1989 than in any year since 1932 (Niebauer et al. 1994; T. Royer, University of Alaska Fairbanks, personal communication). Effects of this reduced flow would include a reduction and delay in the onset of primary productivity (Royer, personal communication), which might have translated into reduced and delayed production by higher-trophic-level consumers such as murres. Such effects may have been attenuated with distance to colonies at Cape Pierce and Bluff. Estimated flow of the ACC returned to long-term average levels by 1993 (Royer, personal communication).

On a broader time scale, there is much evidence (see below) to suggest that the availability of forage fish species was much reduced in the late 1980s and early 1990s, and this may have had a detrimental effect on the reproductive biology of many piscivorous seabirds and marine mammals in the Gulf of Alaska during this time period.

In summary, a number of hypotheses can be advanced to explain the reduction in murre breeding success and delayed breeding phenology observed at "affected" colonies in years immediately after the oil spill. None are mutually exclusive, and it is impossible to segregate possible effects of oil pollution (reduced breeding densities, differential age-class effects, oil toxicity) from natural effects (food stress, oceanographic anomalies). However, the concordance between murres breeding in widely separated colonies within the ACC and evidence for broad-scale changes in marine food webs, suggest that natural factors were already having a strong negative influence on murres at "affected" colonies at the time of the spill and for some years later.

Changes in the Marine Environment

Oceanography and Fish Populations

Long-term oscillations in seawater temperatures in the northern North Pacific are well described (Niebauer 1983; Royer 1993). Water temperatures in the upper 250 m of the water column changed from being colder than average through the 1970s to warmer than average through the 1980s (Figure 4). The transition occurred around 1980. Niebauer (1983) linked these changes with El Niño Southern Oscillation (ENSO) events and shifts in
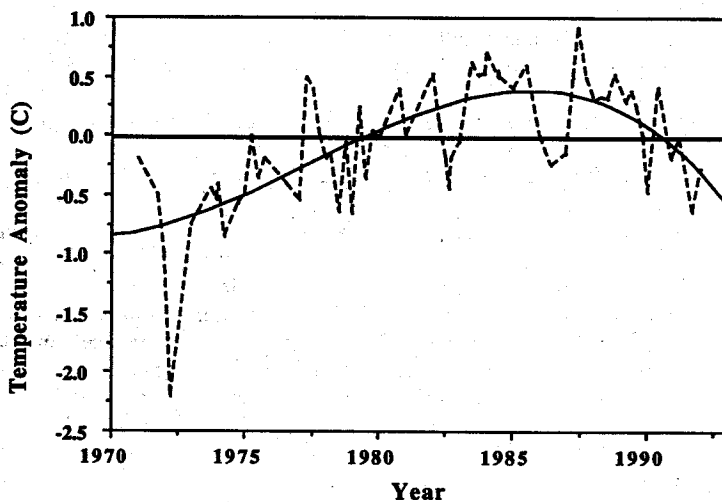
FIGURE 4.—Seawater temperature anomalies at 250-m depth in coastal waters of the northern Gulf of Alaska. Solid curved line shows third-order polynomial fit. (Redrawn from Royer 1993.)

the location and intensity of the Aleutian low pressure cell. He suggested that the shift in ocean conditions that occurred in the late 1970s was triggered by a strong 1976 ENSO event. Royer (1993) showed that this sea temperature cycle is correlated with an 18.6-year luni-solar tidal cycle. He further suggested that it could have important consequences for regional biological populations that are thermally sensitive.

Owing to an effect on metabolic rates, sea temperature anomalies of less than 2°C are sufficient to alter predator–prey relationships among fishes and cause major fluctuations in fish stocks (Laevastu 1984). Perhaps because of this (Albers and Anderson 1985), because many fishes have fairly narrow temperature preferences (e.g., capelins; Methven and Piatt 1991), and for other reasons yet to be determined, the composition and abundance of fish populations along the Alaska Peninsula changed abruptly in the late 1970s as seawater temperatures increased.

A 21-year time series of scientific trawl catches (Figures 5 and 6) in Pavlov Bay indicates that northern shrimp *Pandalus borealis* and capelins virtually disappeared between 1978 and 1979, while walleye pollock *Theragra chalcogramma*, Pacific cod *Gadus macrocephalus*, and flatfish populations increased greatly and persisted throughout the 1980s (Anderson 1991; P. J. Anderson, S. A. Payne, and B. A. Johnson, National Marine Fisheries Service, unpublished data). Mature pollock and cod stock fluctu-

ations as determined by commercial fishery statistics show the same trends (Alverson 1992). The community transition was marked by abrupt changes in abundance of many other species as well (e.g., humpy shrimp *Pandalus goniurus*, longsnout prickleback *Lumpenella longirostris*, Pacific sandfish *Trichodon trichodon*, flathead sole *Hippoglossoides elassodon*, yellowfin sole *Pleuronectes asper*, and eulachon *Thaleichthys pacificus*; Anderson, Payne, and Johnson, unpublished data). This change in community composition was accompanied by about a 50% decrease in overall fish biomass.

The Pavlov Bay study is the longest continuous survey conducted at a single site in the Gulf of Alaska by the National Marine Fisheries Service (NMFS). But how applicable are these observations to other areas of the Gulf of Alaska? The National Marine Fisheries Service conducted trawls using the same gear in numerous bays, offshore gullies, and island passes from Unimak Pass to Castle Cape. Using trawl nets with the same design, the Alaska Department of Fish and Game (ADFG) and NMFS also sampled areas from Castle Cape to Cape Douglas (Cook Inlet), and more than 5,000 trawls were conducted in the bays and gullies around Kodiak and Afognak islands during 1969–1994. Analysis of these data are in progress. All surveys conducted in the western and central Gulf of Alaska reveal the same trend: Beginning around 1978, abrupt changes occurred in the species composition of trawl catches, and a variety of forage fishes such as cape-
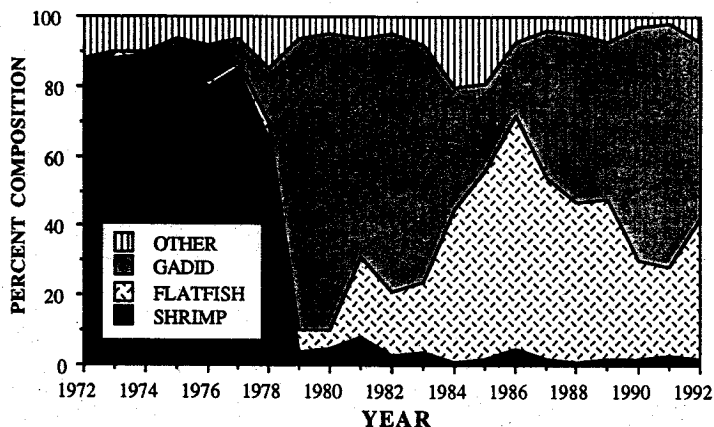
FIGURE 5.—Long-term changes in species composition (percent by weight) of taxa caught by midwater shrimp trawls in Pavlof Bay, Alaska, 1972–1992. (Taken from Anderson et al., unpublished.)

lin virtually disappeared from survey catches (Anderson et al., unpublished). Similar trends have been noted during 1969–1994 from ADFG shrimp trawls in Kachemak Bay (G. Kruse, ADFG personal communication).

In addition to natural factors influencing fish populations, human fisheries have probably had a major impact on trophic relationships in the Gulf of Alaska. During 1964–1994, ever-expanding domestic and foreign fisheries for salmon *Oncorhynchus* spp., Pacific herring *Clupea pallasi*, Atka mackerel *Pleurogrammus monopterygius*, walleye pollock, Pa-

cific cod, Pacific halibut *Hippoglossus stenolepis*, flounders, shrimp, crab, and other species have extracted millions of tons of biomass from the Gulf of Alaska (Alverson 1992). The implications of this massive interference in natural food web relationships are unclear (Springer 1992). Large-scale removal of forage species such as herring and Atka mackerel probably has a direct impact on their predators (Alverson 1992). In some cases, removal of large predatory fish might actually benefit marine birds and mammals that compete for forage fish (Winters and Carscadden 1978; Alverson 1992;
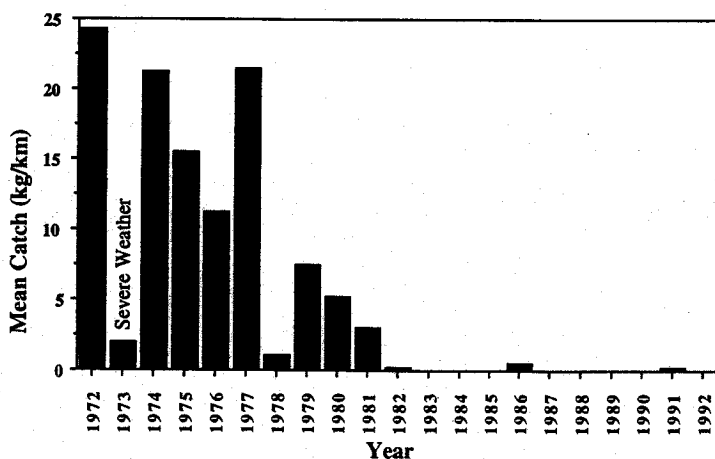

FIGURE 6.—Decline in mean catch-per-effort (kg/km) of capelins in midwater shrimp trawls in Pavlof Bay, Alaska, 1972–1992. Low catches in 1973 resulted from severe weather conditions during surveys. (Taken from Anderson et al., unpublished.)

Springer 1992). Conversely, the artificial introduction of large numbers of salmon from fish hatcheries may have a detrimental effect on competing predators. Because of environmental factors and management practices, salmon stocks were at record-high levels throughout the 1980s (Alverson 1992).

Marine Birds and Mammals

Abrupt changes in marine fish communities in the northern Gulf of Alaska are reflected in the diets and population biology of many marine birds and mammals. We consider here the diets of five abundant seabird species in the northwest Gulf of Alaska from samples ($N = 1,231$) collected during the Outer Continental Shelf Environmental Assessment Program (OCSEAP) (1975–1978; Sanger 1986) and in 1988–1991 ($N = 560$; Piatt, unpublished data). Some caution is required in comparing these samples because they were collected opportunistically at varying times of the year and in many different locations. Most OCSEAP samples were obtained in the Kodiak Island area, but locations sampled in both study periods included Prince William Sound, Kachemak Bay, Kodiak Island, the Semidi Islands, and the Shumagin Islands. In both study periods, samples were collected mostly during the summer breeding season.

Capelins were the dominant prey of seabirds in the late 1970s (Figure 7) but were absent or much reduced in seabird diets in the late 1980s and early 1990s. Capelins were replaced by Pacific sand lances *Ammodytes hexapterus* and pollock. Preliminary analysis of seabirds ($N = 450$) collected in 1992–1993 revealed a similar scarcity of capelins in diets (Piatt, unpublished data). Likewise, diets of northern fur seals *Callorhinus ursinus*, northern sea lions *Eumetopias jubatus*, and harbor seals *Phoca vitulina* collected in the 1970s were rich in fatty forage fish such as capelin and herring (Pitcher 1980, 1981; Castellini 1993). These prey were rare in stomachs of fur seals and Stellar sea lions collected in the 1980s (Alverson 1992; Castellini 1993; R. Merrick, NMFS, personal communication).

Coupled with these changes in diet, and probably because of them (Castellini 1993; Springer 1993), there have been marked changes in the population ecology of several marine bird and mammal species in the Gulf of Alaska. For example, breeding success of black-legged kittiwakes *Rissa tridactyla* at colonies in the Gulf of Alaska declined dramatically through the 1980s (Figure 8; Hatch et al. 1993; Hatch and Piatt 1995). Kittiwake populations have declined (about 50%) at Middleton Island since about 1980. Common murre populations have declined by up to 90% at many colonies outside the oil spill zone (Figure 2, Table 1) and were declining at some affected colonies before the spill occurred. Results of Prince William Sound boat surveys conducted in 1989–1991 suggest that there have been major declines (50–95%) in populations of 15 different coastal and marine bird species since surveys conducted in 1972–1973 (Klosiewski and Laing 1994). Species that have declined significantly include cormorants (−95%), *Larus* gulls (−69%), kittiwakes (−57%), pigeon guillemots *Cepphus columba* (−75%), marbled and Kittlitz's murrelets *Brachyramphus* spp. (−68%), and horned puffins *Fratercula corniculata* (−65%). Similarly, analysis of Christmas Bird Count data suggests that marbled murrelet populations in the Gulf of Alaska have declined by over 50% since the early 1970s (Piatt and Naslund 1995).

As another indication that food has been limiting in recent years, several large-scale die-offs of seabirds, mostly of surface-feeding species, have been observed in the Gulf of Alaska during 1983–1993, most notably in 1983, 1989, and 1993 (Hatch 1987; Piatt et al. 1990; D. R. Nysewander and J. L. Trapp, U.S. Fish and Wildlife Service, unpublished data). In March 1993, an estimated 100,000 common murres died throughout an area spanning southeast Alaska to the Alaska Peninsula (Piatt and van Pelt 1993). Starvation was determined to be the proximate cause of death. In contrast, there were no reported die-offs in the 1970s since Bailey and Davenport's (1972) report of a massive murre die-off along the Bering Sea side of the Alaska Peninsula in 1970.

Marine mammals have exhibited similar signs of food stress in recent years. Harbor seals at Tugidak Island in the Gulf of Alaska declined by about 85% between 1976 and 1988 (Figure 9; Pitcher 1990). Northern sea lion populations declined (Figure 9) by 36% in the Gulf of Alaska between 1977 and 1985 (Merrick et al. 1987) and by another 59% between 1985 and 1990 (Loughlin et al. 1992; Castellini 1993). Northern fur seals declined by about 35% by 1986 from their average numbers in the 1970s, although numbers had rebounded somewhat (20%) by 1990 (Castellini 1993). Associated with the declines in northern sea lions are declines in birth rate, fewer breeding females, fewer pups, decreased adult body condition, decreased juvenile survival, and a change in population age structure (Merrick et al. 1987; Loughlin et al. 1992). Declines in marine mammal populations may result in part
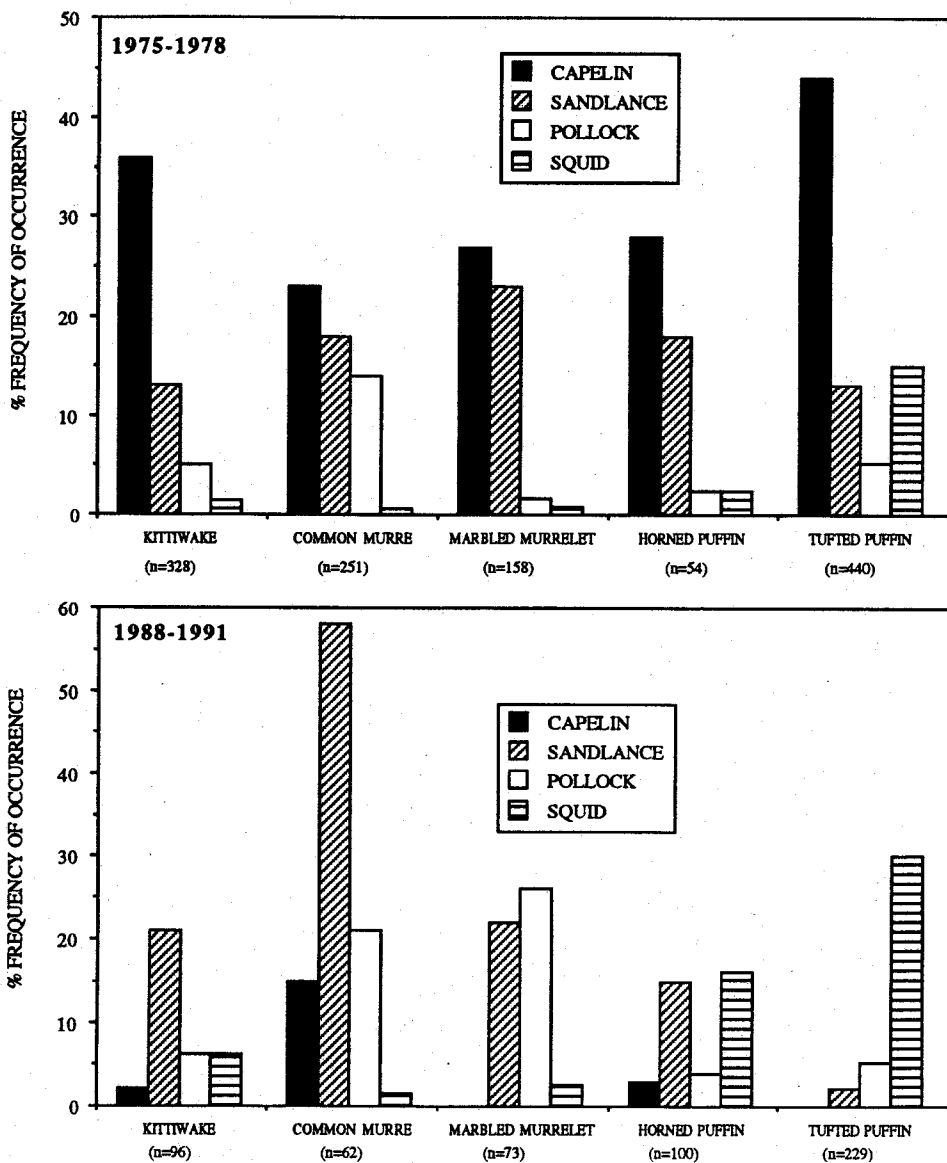
FIGURE 7.—Change in diet composition (% frequency of occurrence) of five seabird species collected in the Gulf of Alaska between 1975–1978 (upper panel; Outer Continental Shelf Environmental Assessment Program data; Sanger 1986) and 1988–1991 (lower panel; J. Piatt and A. Springer, unpublished data).

from harvest, incidental catch in fishing gear, and disease, but the concensus among researchers is that changing food availability (lower quality or biomass) is the most likely cause of recent declines (Castellini 1993).

Conclusions

A Changing Marine Environment

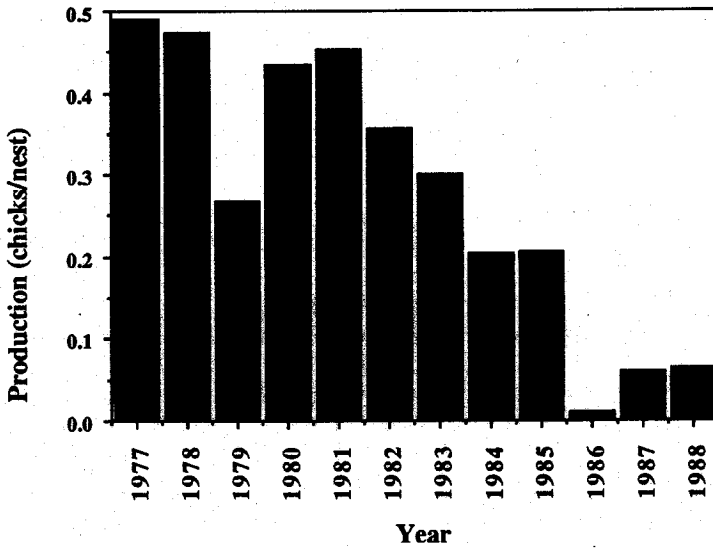Various independent data indicate that there has been an abrupt shift in the marine ecosystem of the

FIGURE 8.—Declining productivity of black-legged kittiwakes in the Gulf of Alaska, 1976–1989. Data from Middleton, Barren, and Semidi islands and Chiniak Bay (Hatch et al. 1993) were grouped for this analysis and plotted here as 3-year running-means from 1977 to 1988.

Gulf of Alaska between the mid-1970s and the mid-1990s. This shift has been manifested by marked changes in the composition of marine fish communities, reduced forage fish biomass, and dramatic changes in the population ecology of higher vertebrates that depend on those fish populations. Un-

like short-term phenomena such as the El Niño, which may disrupt marine food webs and diminish seabird productivity for 1- to 2-year time periods (Ainley and Boekelheide 1990), this shift represents a more pervasive and persistent change in the ecosystem.
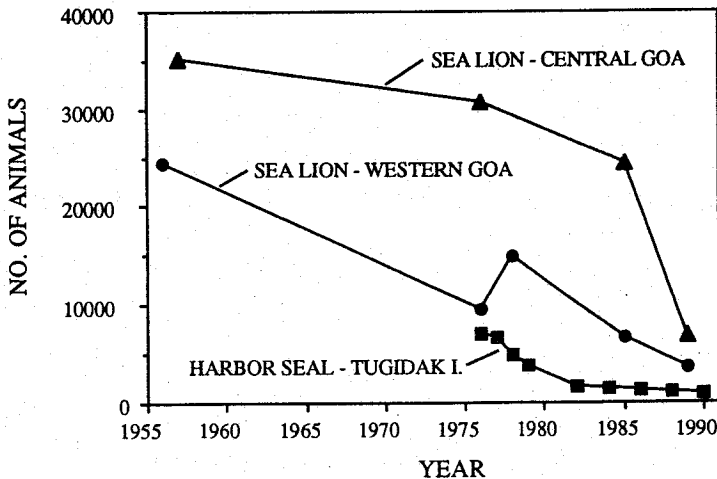

FIGURE 9.—Declining populations of northern sea lions and harbor seals in the Gulf of Alaska (GOA). (Derived from Pitcher 1990, Merrick et al. 1987, and Loughlin et al. 1992.)

It appears that a "change of state" was initiated in 1976, when atmospheric circulation in the north Pacific shifted and remained that way until the late 1980s (Trenberth 1990; Kerr 1992). Effects of this climate shift were evident in a number of environmental variables measured throughout the eastern North Pacific between 1968 and 1984 (Kerr 1992). It may have taken 3–5 years for this change of state to be manifested by changes in water temperatures, fish populations, and seabird demography in Alaska. Atmospheric and ocean climate conditions may now be returning to those observed before 1976 (Figure 1; Trenberth 1990; Royer 1993).

Although they do not appear to be synchronized with events in the Gulf of Alaska, similar temporal relationships between water temperatures, fish stocks, seabirds, and marine mammals have been observed in the Bering Sea (Alverson 1992; Springer 1992; Decker et al., in press). Productivity of seabirds nesting on the Pribilof Islands started declining in about 1978, as water temperatures rose above average and an unusually large year-class of pollock appeared. Seabird productivity remained low through the 1980s, while pollock stocks increased dramatically. Diet composition of murres and kittiwakes changed significantly, and indicator species such as capelins and hyperiid amphipods largely disappeared from diets in the 1980s (Decker et al., in press). By the late 1980s, seabird productivity was increasing again as pollock stocks declined. As in the Gulf of Alaska (above), a strong negative relationship between pollock biomass and kittiwake production may be an indication that predators compete for forage fish and that food webs are regulated by "top-down" interactions (Springer 1992). Alternatively, forage fish, pollock, kittiwakes, and other predators may be responding in their own fashion to changing oceanographic conditions and primary production ("bottom-up" control; Springer 1992).

Whatever the mechanism, natural long-term cycles in marine productivity may account for much of the variation observed in seabird population parameters. For example, Aebischer et al. (1990) demonstrated a remarkable similarity between long-term (33-year) trends in wind patterns, the abundance of phytoplankton, zooplankton, and Atlantic herring *Clupea harengus*, and kittiwake clutch size, phenology, and chick production in the North Sea. All these measures of biological production declined from about 1955 to the late 1970s, and have been increasing since that time.

Murre Population Declines

The magnitude of seabird mortality (about 250,000 killed) from the *Exxon Valdez* oil spill was high enough to expect that some seabird populations, especially those of murres, were damaged to a degree that was biologically significant. We conclude, however, that (1) coastal murre colonies under the influence of the ACC were already under stress and declining when the oil spill occurred; (2) a high toll of murres from the spill must have added to this decline, resulting in an overall decline of about 40% at affected colonies between the late 1970s and early 1990s; and (3) the quality and quantity of prespill colony data do not allow us to distinguish between effects of the spill and natural responses to a changing marine environment.

The magnitude of murre declines observed in the Gulf of Alaska are not unique. Massive declines (−70 to −90%) of common murre populations occurred quickly (1985–1987) in the Barents Sea, apparently in response to a collapse of capelin stocks (Vader et al. 1990). Murre populations at 28 colonies on the outer coast of Washington plummeted (about −90%) between 1982 and 1983, and populations have not recovered as of 1994 (Ainley et al. 1994). Similarly, common murre populations in central California declined 53% over a 6-year period (1980–1986), and populations are recovering very slowly (Takekawa et al. 1990; Ainley et al. 1994). The 1982–1983 ENSO event, gill-net mortality, oil spills, and competition from commercial fisheries are all implicated in the decline of murres in California and Washington.

In all these cases, it has not been possible to quantitatively apportion blame to any one cause of population declines. It is increasingly clear that large-scale fluctuations in prey abundance, usually mediated by oceanographic phenomena and commercial fisheries, have far greater influence on seabird population dynamics than local, one-time events such as oil spills. There is much circumstantial evidence to indicate that chronic oil pollution has long-term effects on seabird populations (Piatt et al. 1991), but it has been difficult to demonstrate long-term damages in acute cases (but see Stowe 1982).

Murre Breeding Success and Phenology

None of the postspill murre studies can show conclusively that the observed postspill reductions in murre breeding success and delayed phenology resulted directly from the oil spill. We can reasonably speculate about potential effects of changing

demography and breeding densities, and toxic effects of oil, but a more plausible hypothesis is that changes in the marine environment of the Gulf of Alaska were primarily responsible for the observed changes in murre breeding biology.

Such effects have been documented repeatedly for murres and other seabirds in response to food stress or changes in oceanographic conditions (e.g., Boersma 1978; Hedgren 1979; Anderson and Gress 1984; Monaghan et al. 1989; Ainley and Boekelheide 1990; Murphy et al. 1991; Wilson 1991; Duffy 1993; Uttley et al. 1994). For example, median egg-laying of murres, Cassin's auklets *Ptychoramphus aleuticus*, and pigeon guillemots at the Farallon Islands were observed to be delayed by 2–6 weeks in association with ENSOs or anomalously warm water temperatures (Ainley and Boekelheide 1990). For common murres, mean dates of egg-laying varied by 1 month during 12 years of study (Boekelheide et al. 1990). Similarly, feeding rates and breeding success of several species at the Farallons declined markedly during ENSO events.

Reports of complete murre breeding failures are rare, however, and under a wide range of moderate to good conditions they exhibit low variance in breeding success—much lower than coexisting species (Piatt 1987, 1990; Boekelheide et al. 1990; Hatch and Hatch 1990b). For example, coefficients of variation in common murre breeding success at the Semidi (16%) and Farallon (29%) islands are far lower than those of coexisting kittiwakes (101%) and pelagic cormorants (85–97%). This situation probably occurs because murres can buffer against fluctuations in prey abundance by spending more or less time foraging (Piatt 1987, 1990; Burger and Piatt 1990; Uttley et al. 1994).

Despite their buffering capacity, murres at colonies in the ACC exhibited low levels of breeding success and markedly delayed phenology in 1989 and 1990. Kittiwakes also failed (0.0–0.06 chicks/nest) in 1989 (Hatch et al. 1993—no data for 1990) at most colonies in the Gulf of Alaska (Middleton, Barren, and Semidi islands) and Bering Sea (Cape Pierce, Pribilof Islands, and Bluff). Two different factors may have influenced murre foraging success in these years. First, major long-term changes in forage fish availability (above) may have already pushed murres to the limits of their capacity to deal with fluctuations in prey abundance in the late 1980s and early 1990s. Second, unusually low-volume transport of the ACC (above) may have reduced and delayed primary productivity in the coastal marine environment (Niebauer et al. 1994;

Royer, personal communication), leading to a similar delay and reduction in productivity of murres.

Perspective on Oil Spill Impacts and Recovery

Our inability to demonstrate unequivocal long-term effects of the oil spill on murre populations should not lead us to a conclusion that there were none (e.g., Boersma et al. 1995; Erickson 1995). Wiens (1995) argued that biological systems are so variable that the effects of oil mortality were probably biologically insignificant and, in any case, statistically undetectable. We would argue that we lack the necessary data to draw strong conclusions one way or the other. We reach the heights of human arrogance when we assume that eliminating hundreds of thousands of healthy seabirds was unimportant to a species simply because we had few data on some narrowly defined parameters with which to "assess" damages. Furthermore, impacts of a single event like the *Exxon Valdez* oil spill may over the long term be additive to other sources of mortality (e.g., from gill-nets, starvation) and should not be evaluated in isolation (Piatt et al. 1991). On the other hand, the one-time loss of 7% of gulf murre populations is not a drastic occurrence for a species as resilient as the common murre. At least this percentage of murre populations dies annually from natural mortality (Birkhead and Hudson 1977; Sydeman 1993).

When will murre populations recover? Some early predictions (e.g., Piatt et al. 1990) about 20- to 70-year recovery times were based on demographic models (Ford et al. 1982) that assumed stability of the marine ecosystem. As a coauthor of these original models, Wiens (1995) more recently points out that this assumption is invalid. Nonetheless, evidence suggests that current conditions in the Gulf of Alaska are not conducive to a more rapid recovery of murre populations. Until we achieve a much better understanding of long-term cycles in the marine environment and factors influencing seabird demography, predictions about long-term impacts of oil pollution on seabird populations will remain largely speculative.

One positive consequence of the *Exxon Valdez* oil spill is that it forced us to gather more and better data on neglected seabird populations. Maybe we will be able to improve quantification of effects during the next oil spill. Meanwhile, the data collected on murres and other taxa provide insight into a phenomenon of greater impact and importance, namely, long-term changes in the marine ecosystem of the Gulf of Alaska. We need to study further the

mechanisms that have led to chronic population declines of shrimp (>95%), capelins (>95%), cormorants (>90%), kittiwakes (>50%), murres (>50%), marbled murrelets (>60%), puffins (>60%), harbor seals (>85%), and sea lions (>90%) in some areas of the Gulf of Alaska from the mid-1970s to the mid-1990s.

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